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## ON THE MUTUAL RELATIONS OF THE BUNOTHERIAN MAMMALIA.

BY E. D. COPE.

The name *Bunotheria* was proposed by me for a series of Mammalia which resemble in most technical characters the Edentata and the Rodentia. That is, they agree with these orders in having small, nearly smooth cerebral hemispheres, which leave the olfactory lobes and cerebellum entirely exposed, and in some instances the hemispheres do not cover the mesencephalum also. From the two orders in question, however, they are easily distinguished. Their enamel-covered teeth separate them from the Edentata, while the articulation of the lower jaw is different from that found in the Rodentia. It is a transverse ginglymus, with a postglenoid process in the *Bunotheria*, as distinguished from the longitudinal groove, permitting anteroposterior motion, of the Rodentia.

Such a group as is thus characterized will include two existing groups recognized as orders—the Prosimiæ and the Insectivora. The latter group has always been a crux to systematists, and when we consider the skeleton alone, as from the standpoint of the palæontologist, the difficulty is not diminished. Various extinct types discovered in latter years, chiefly in the Eocene formations, have been additions to this intermediate series of forms, giving even closer relations with the orders already adjacent; *i. e.*, the Edentata, the Rodentia, the Prosimiæ, and the Carnivora. As is known, the groups corresponding to these orders have been named respectively the Tæniodonta, Tillodonta, Mesodonta, and Creodonta. With great apparent diversity, these suborders show unmistakable gradations into each other and the two recent orders already mentioned. As such, I may mention *Psittacotherium*, which relates the Tæniodonta and Tillodonta; *Esthonyx*, which relates the Tillodonta with nearly all the other suborders; *Achænodon*, which connects Creodonta and Mesodonta, and *Cynodontomys*, which may be Mesodont or Prosimian. Then the existing *Chiromys* most certainly connects Tillodonta and Prosimiæ.

My original definitions of the suborders of the Mesodonta, given in vol. ii of the U. S. Geological Survey under Capt. G. M. Wheeler, p. 85, omitted the Prosimiæ, and embraced a number

of characters whose significance must be reëxamined. Thus it is impossible to characterize the Creodonta as lacking a trochlear groove of the astragalus, in view of the form of that element in *Mesonyx* and *Mioclænus*, where the groove is more or less distinct. It is impossible to distinguish the Insectivora from the Creodonta by the deficiency of canine and large development of incisor teeth. In *Rhynchocyon* the canines are large, and the superior incisors wanting, while in *Centetes* the arrangement of these teeth is precisely as in the Creodonta. As to the large *Achænodon* and other *Arctocyoniidæ*, I find no characters whatever to distinguish them from the generally small Mesodonta.

In view of these inconsistencies, I have reëxamined the subject, and find the following definitions to be more nearly coincident with the natural boundaries of the divisions of this large order. The importance of the character of the tritubercular superior molar has recently impressed me (see Proceedings of the Academy, 1883, p. 56), as it had previously done Prof. Gill. This zoologist has already distinguished two divisions of the Insectivora (without the *Galeopithecidæ*), by the forms of the superior molar teeth. The first possesses quadritubercular molars above, the second tritubercular. That these types represent important stages in the development of the molar dentition I have no doubt. These characters far outweigh in importance those expressing the forms of the skull, matters of proportion only, with which a few systematists unnecessarily overload their diagnoses. Such characters are of little more than specific value, and serve to obscure the mind of the inquirer for a true analysis. They may be used empirically, it is true, to determine relationships when the diagnostic parts are wanting.

I propose to transfer the Insectivora with tritubercular superior molars to the Creodonta, in spite of the fact that some of them (*Mythomys*, *Solenodon*, *Chrysochloris*) have but weakly developed canine teeth, and *Chrysochloris* has large incisors. As an extreme form, *Esthonyx* will follow, standing next the Tillodonta. It will then be necessary to transfer the Arctocyoniidæ and all the Mesodonta to the Insectivora, where they will find affinity with the *Tupæidæ*. These have well-developed canines and small incisors, as in the extinct groups named. The *Chiromyidæ* must be distinguished from all of the other suborders, on account of its rodent-like incisors, combined with its lemur-like feet.

The characters of the six suborders will then be as follows :

I. Incisor teeth growing from persistent pulps :

Canines also growing from less persistent pulps, agreeing with external incisors in having molariform crowns ; I. *Tæniodonta*.

Canines rudimental or wanting ; hallux not opposable ;

II. *Tillodonta*.

Canines none ; hallux opposable ;

III. *Daubentonioidea*.

II. Incisor teeth not growing from persistent pulps :

Superior true molars quadrituberculate ; hallux opposable ;

IV. *Prosimiæ*.

Superior true molars quadrituberculate ; hallux not opposable ;

V. *Insectivora*.

Superior true molars trituberculate or bituberculate ;<sup>1</sup> hallux not opposable :

VI. *Creodonta*.

While the above scheme defines the groups exactly, and, so far as can now be ascertained, naturally, I do not doubt but that future research among the extinct forms will add much necessary information which we do not now possess. It is possible that the group I called *Mesodonta* may yet be distinguished from the *Insectivora* by characters yet unknown. But I cannot admit any affinity between this group and any form of "*Pachyderms*," as suggested by Filhol, or of *Suillines*, as believed by Lyddeker.<sup>2</sup> Such suppositions are in direct opposition to what we know of the phylogeny of the *Mammalia*. These views are apparently suggested by the *Bunodont* type of teeth found in various *Mesodonta*, but that character gives little ground for systematic determination among Eocene *Mammalia*, and has deceived palæontologists from the days of Cuvier to the present time. The only connecting point where there may be doubt as to the ungulate or unguiculate type of a mammal is the family *Periptychidæ*, of the suborder *Condylarthra*. The suborder *Hyracoidea* may furnish another index of convergence.

<sup>1</sup> The internal tubercle is wanting in the last two superior molars in *Hyænodon*. This genus, of which the osteology remains largely unknown, has been stated by Gervais to possess a brain of higher type than the *Creodonta*. Prof. Scott, of Princeton, is, however, of the opinion that this determination is erroneous, and that *Hyænodon* is a true *Creodont* in this and other respects. If so, the genus will perhaps enter the *Amblyctonidæ*.

<sup>2</sup> *Memoirs Geological Survey India*, Ser. x, 1883, p. 145.

The families included in these suborders will be the following :

TÆNIODONTA. *Calamodontidæ*; *Ectoganidæ*.

TILLODONTA. *Tillotheriidæ*.

DAUBENTONIOIDEA. *Chiromyidæ*.

PROSIMLÆ. *Tarsiidæ*; (?) *Anaptomorphidæ*; (?) *Mixodectidæ*; *Lemuridæ*.

INSECTIVORA. *Soricidæ*; *Erinaceidæ*; *Macroscelidæ*; *Tupæidæ*; *Adapidæ*; <sup>1</sup> *Arctocydonidæ*.

CREODONTA. *Talpidæ*; *Chrysochlorididæ*; *Esthonychidæ*; *Centetidæ* (= *Leptictidæ* olim); *Oxyænidæ*; *Miacidæ*; *Amblycytonidæ*; *Mesonychidæ*.

I at one time called this order by the name *Insectivora*, a course which some zoologists may prefer. But a name should as nearly as possible adhere to a group to which it was first applied, and whose definition has become currently associated with it. Such an application is correct in fact, and is a material aid to the memory. There are various precedents for the adoption of a new general term for a group composed of subordinate divisions which have themselves already received names.

In order to determine the number of internal tubercles in some of the *Insectivora*, so as to ascertain the affinities of some questionable genera, it is first necessary to examine the homologies of the cusps of the molar teeth. The opossums are characterized by the presence of three longitudinal series of tubercles on the superior molar. The homologies of these cusps are rendered clear by the character presented by the fourth superior premolar, where the anterior intermediate is wanting. The external cusps are really such, and are not developed from a cingulum external to the true external cusps, as appears at first sight to be the case with such animals as the *Talpidæ*. The intermediate cusps are really such, although the posterior looks like the apex of a V-shaped external cusp. In *Peratherium* the external cusps are smaller than in *Didelphys*, and the intermediate V's so much

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<sup>1</sup> Two species of *Pelycodus* must be removed from this genus and family, and be placed in the *Creodonta* with *Miocænus*. They are the *P. pelvidens* and *P. angulatus*, which have the posterior inner tubercle of the superior molars, a mere projection of the cingulum. I place them in a new genus which differs from *Miocænus* in the possession of an internal cusp of the fourth inferior premolar, under the name of *Chriacus*; type *C. pelvidens*.

better developed, that the type is much like that of the *Talpidæ*, in whose neighborhood I originally referred it.

This leads to a consideration of the question of the homologies of the cusps in the genera of the old order of *Insectivora* proper, and of the *Creodonta*. Mr. St. George Mivart has briefly discussed the question, so far as relates to the former group.<sup>1</sup> He commences with the primitive quadrituberculate type presented by *Gymnura* and *Erinaceus*, and believes that the external cusps occupy a successively more and more internal position till they come to be represented by the apices of well developed V's, as in the ungulate types. The V's are well developed in several families, and in *Chrysochloris* the two V's are supposed to be united and to constitute almost the entire apex of the crown, while in *Centetes* the same kind of a V forms a still larger part of the crown.

I believe that these conclusions must be modified, in the light of the characters of various extinct genera, and of the genus *Didelphys*. In the first place there is an inherent improbability in the supposition that the external V's of the superior molars of the *Insectivora* have had the same origin as those of the *Ungulata*. The movements of the jaws in the two groups are different, the one being vertical, the other partially lateral. In the one, acute apices are demanded; in the other, grinding faces and edges. We have corresponding V's in the inferior dental series, and we regard those as produced by the connection of alternating cusps by oblique ridges. In homologizing the superior cusps, we have as elements, two external, two intermediate, and two internal cusps. The first are opposite the external roots, and the anterior internal is opposite the internal root.

First, as regards *Centetes* and *Chrysochloris*. Besides the strained character of the hypothesis that supposes the V-shaped summit of the crown to represent two V's fused together, there is good evidence obtainable in support of the belief that the triangle in question is the usual one presented by the *Creodonta*.

This clearly consists of the two external and the anterior internal cusps united by angular ridges. The form is quite the same as in *Leptictis* and *Ictops*, and nearly that of *Deltatherium*, where the external cusps are present. *Centetes* and *Chrysochloris* only differ from these in that the external cusps are wanting. In

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<sup>1</sup> Journal of Anatomy and Physiology, ii, 138, figures.

addition, the latter genus presents a rudiment of the posterior inner tubercle, as is seen in *Deltatherium*. An explanation similar to this is admitted by Mr. Mivart to apply to the cusps of the inferior molar of *Centetes*. It remains to ascertain whether the cusp in this genus, *Chrysochloris*, etc., represents an intermediate or not.

Secondly, as regards the *Talpidæ* and *Soricidæ*, where the external V's are well marked. If we examine the external cusps in the genus *Didelphys*, we find that the posterior one becomes gradually more anterior in its position, until on the second true molar it stands largely above the interspace between the roots, instead of over the posterior root. It will also be seen that the anterior intermediate tubercle is distinct, and of insignificant proportions, while the posterior intermediate is large and is related to the posterior external, as is the apex of a V to its anterior base. In this arrangement I conceive that we have an explanation of the V's of the *Talpidæ* and *Soricidæ*. The first true molar of *Scalops* is a good deal like that of *Didelphys*, but the anterior cusp is larger and there is no anterior intermediate cusp, while the posterior external is of reduced size. The posterior V is better developed than in *Didelphys*, but is composed in the same way, of a posterior intermediate cusp, and a posterior external with a posterior heel. These are united by stronger ridges in *Scalops*, *Condylura* and *Blarina*, than in *Didelphys*. On the second true molar in *Scalops*, a V represents the anterior external cusp of the first true molar. Whether this V has a constitution like the posterior one, *i. e.*, is composed of external and intermediate cusps joined, is difficult to determine; but it is probably so constituted. It seems to be pretty clearly the case in *Blarina*, where the fourth premolar and first true molar may be compared, with a resulting demonstration of the correctness of this view. In *Condylura*, the V's have become more developed and the external cusps reduced, so that the analysis is more difficult.

This interpretation applied to *Urotrichus* and *Galeopithecus* gives them quadrituberculate molars, not trituberculate, as determined by Mivart. *Myiomyotis* is tritubercular. The intermediate tubercles are present, but are imperfectly connected with the external, so that V's are not developed (*vide* figures of Mivart and Allman). This genus offers as much confirmation of the homology

here proposed as do the opossums, but it differs from the latter in having the anterior intermediate tubercle the larger, instead of the posterior. *Mystomys* and *Solenodon* also confirm my determination of the homologies in *Centetes*.<sup>1</sup>

In conclusion I give the following synoptic view of the constitution of the superior molar teeth in various genera of the *Bunoheria*.

## CUSPS PRESENT.

External. Intermediate. Two internal.	External. No intermediate. Two internal.	External. Intermediate One internal.	External. No intermediate. One internal.	No external. No intermediate. Two internal.	No external. No intermediate. One internal.
Adapidae.	Gymnura.	Mystomyidae	Mesonyx.	Chrysochloris (2d internal rudimentary)	Centetes.
Tupæidae.	Erinaceus.	Miocænus.	Leptictis.		
Galeopithecidae	Macroscelididae	Miacis.	Stypolophus.		
Soricidae.		Talpidae.	Oxyæna.	Solenodon. (do.)	
Urotrichus.		(Didelphys.)	Chriacus.		
		(Canis.)	Deltatherium		
			Esthonyx. (2nd internal rudimentary)		

<sup>1</sup> This view was first advanced by the writer in the Annual Report U. S. Geol. Survey Terrs., 1873 (74), p. 472.